Human variation in pelvic shape and the effects of climate and past population history

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Running title: pelvic variation, climate and genetic drift

ABSTRACT
The human pelvis is often described as an evolutionary compromise (obstetrical dilemma) between the requirements of efficient bipedal locomotion and safe parturition of a highly encephalized neonate, that has led to a tight fit between the birth canal and the head and body of the foetus. Strong evolutionary constraints on the shape of the pelvis can be expected under this scenario. On the other hand, several studies have found a significant level of pelvic variation within and between human populations, a fact that seems to contradict such expectations. The advantages of a narrow pelvis for locomotion have recently been challenged, suggesting that the tight cephalo-pelvic fit might not stem from the hypothesized obstetrical dilemma. Moreover, the human pelvis appears to be under lower constraints and to have relatively higher evolvability than other closely related primates. These recent findings substantially change the way in which we interpret variation in the human pelvis, and help make sense of the high diversity in pelvic shape observed within and among modern populations. A lower magnitude of covariance between functionally important regions ensured that a wide range of morphological variation was available within populations, enabling natural selection to generate pelvic variation between populations living in different environments. Neutral processes such as genetic drift and differential migration also contributed to shaping modern pelvic diversity during and after the expansion of humans into and across the various continents.

Key words: pelvis, climate, evolvability

The last few years have seen a remarkable increase in research on the evolution of the human pelvis and on the factors that explain pelvic shape variation in modern human populations. The classic model of the human pelvis as a strict compromise between locomotory and obstetrical requirements, omnipresent in anthropology textbooks, has been challenged from different directions, first of all by calling into question the underlying idea of a conflict between a wide, obstetrically capacious pelvis and efficient bipedal locomotion. The accompanying assumption of strong evolutionary constraints on the shape of the pelvis has also been disputed, and new evidence has emerged of ample geographic variation in pelvic shape within our species. While geographic variation in the pelvis has often been explained as climatic adaptation, new research has revealed the overarching effects of neutral evolutionary processes in generating population differences in pelvic shape. This review integrates old and new evidence to draw a sketch of the current state of understanding of the origins of human pelvic shape variation.

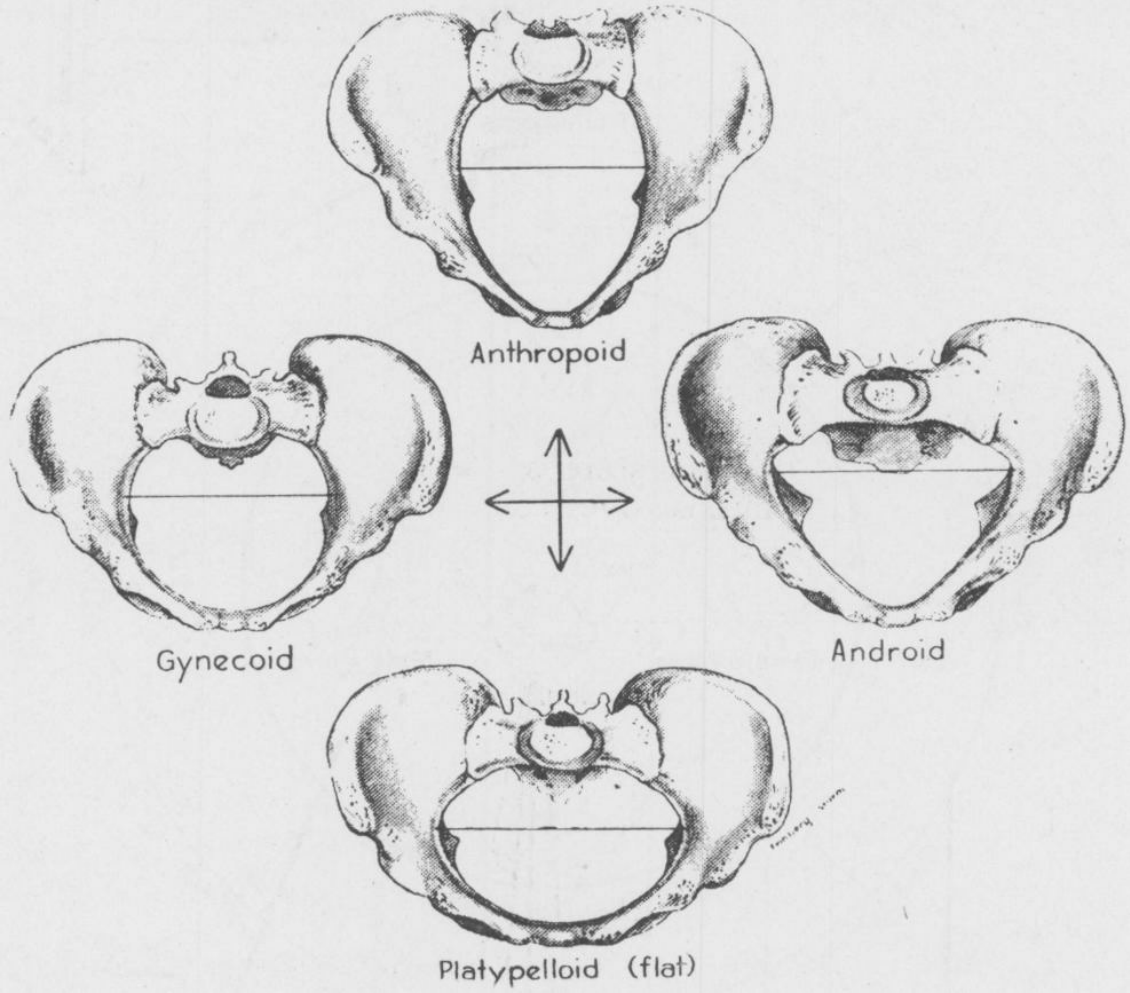

Fig. 1. Caldwell and Moloy's pelvic types (Caldwell and Moloy, 1938; from an unknown original source).

Early observations of pelvic variation and the "obstetrical dilemma" hypothesis

Humans originated in Africa, but have dispersed globally and colonised a variety of environments. As a consequence, modern human populations show a genetic and phenotypic variation that is geographically structured. For centuries, and up to the middle of the 20th century, many naturalists and anthropologists made sense of human variation by assigning populations to well-defined groups based on their physical and cultural characteristics. Early studies of human pelvic variation followed this approach, and focused on the prevalence of different pelvic shapes (e.g., Fig. 1) in the various 'races' as well as their obstetric proficiency (e.g., Turner, 1885; Caldwell and Moloy, 1933; Greulich and Thoms, 1938; Allen, 1947a,b). The rounder shape of the canal in some populations (e.g., KhoeSan, Andamanese and Australians) was considered simultaneously to be more primitive and more suitable for childbirth. The transversally more elongated shape of European women, on the other hand, was described as less adept for childbirth being the race farthest from the animal kingdom (Turner, 1885 – who was, incidentally, European). Although the female pelvis was generally assumed to be shaped in accordance to its obstetric functions, it became obvious that it varied in shape between human groups.

Since the mid 20th century, most scholars moved away from a racial categorization of human variation, and pelvic shape became largely discussed as the outcome of evolutionary processes. The human pelvis differs from other apes in several traits, being a shorter and more compact structure, with the ilia curved around the side of the body to form a bowl shape. The peculiar human shape has been associated with a shift to bipedal locomotion early in the hominin lineage (e.g., Bramble and Lieberman, 2004; Grabowski and Roseman, 2015). The need to balance the whole body on one foot at a time, during walking or running, favoured relatively short and narrow hips that would keep the joint of the leg and pelvis close to the sacrum and to the centre of gravity (Lovejoy et al., 1973, 1999; Lovejoy, 1988, 2005). With the evolution of a larger brain size in Middle Pleistocene hominin species (Ruff et al., 1997; Rightmire, 2004), additional changes in the shape of the female pelvis were brought on by the need to give birth to a more encephalized neonate. The conflict between the shape requirements for efficient bipedal locomotion and for the safe passage of the newborn through the pelvic canal was described by Washburn (1960) as an "obstetrical dilemma".

The basic tenet of the obstetrical dilemma is that a narrower bi-acetabular distance, which positions the support of the body closer to the centre of gravity, reduces the rotation of the hip during locomotion and the energy required by the muscles to counteract it, thereby improving efficiency. At the same time, a narrower bi-acetabular breadth would also lead to a less spacious pelvic canal, with an increased risk of foeto-pelvic disproportion and obstructed labour, where the head or body of the neonate does not fit thought the mother's birth canal (Rosenberg, 1992; Wittman and Wall, 2007). The selective pressure for efficient locomotion and the female-specific pressure for a sufficiently large pelvic canal led to a compromise, whereby the female pelvis is larger than the male pelvis, to accommodate the passage of the foetus, but probably less efficient for locomotion. The result of this

compromise is a very tight fit between the newborn's head and shoulders and the mother's birth canal, balancing the two contrasting needs (Schultz, 1949; Leutenegger, 1974; Tague and Lovejoy, 1986; Rosenberg, 1992; Rosenberg and Trevathan, 1995; Trevathan and Rosenberg, 2000; DeSilva, 2011). Adaptations to bipedalism are also considered a likely explanation for the twisted human birth canal, whose main diameter changes in orientation as the foetus moves downwards. The changing geometry of the passage has led to the definition of three different levels of the canal: the inlet, defined as the pelvic brim at the level of the iliopectineal lines and the superior margin of the iliopubic ramus and pubic symphysis; the midplane, defined by the ischial spines, the lower margin of the pubic symphysis and the end of the fourth sacral vertebra; the outlet, defined by the medial margins of the ischial tuberosities, the inferior margin of the pubic symphysis and the end of the sacrum (Fig. 2).

The obstetrical dilemma has also been suggested to be at the root of sexual dimorphism, with obstetric requirements driving sexual differences in the shape and size of the pelvis. The main differences between the sexes relate to the shape of the ilium and of the pubis, where many sexually dimorphic traits are stable across human populations, making the pelvis the best anatomical structure to determine the sex of an individual from the skeleton in archaeological and forensic contexts (e.g., Bass, 1971; Brothwell, 1981; White et al., 2012). Betti (2014) showed, however, that, beyond some shared sexually dimorphic characteristics, human populations differ in the details of pelvic sexual variation (see also Wilson et al., 2015).

All human populations walk bipedally and give birth to similarly encephalized babies; therefore, we expect that the obstetrical dilemma and the same compromise in pelvic shape apply to all populations. If we assume that strong selective pressures led to a tight compromise in the pelvis, we could also expect that strong evolutionary constraints will limit how much pelvic shape can differ between populations. These assumptions seem in contradiction with historical and more recent observations of geographic variation in the shape of the pelvis and the birth canal.

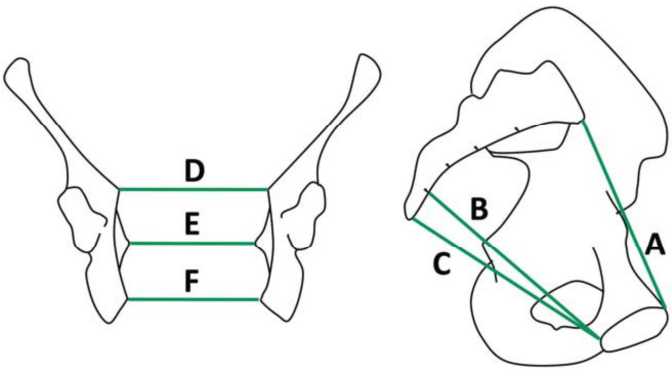

Fig. 2. Diagrams of the three planes of the birth canal (figure redrawn and modified after Tague, 1989; Aiello and Dean, 1990; Kurki, 2007, and others). A, B, C = anteroposterior diameters of the inlet, midplane and outlet, respectively. D, E, F = mediolateral diameters of the inlet, midplane and outlet, respectively.

A re-evaluation of the obstetrical dilemma

Recent studies have challenged one main assumption of the obstetrical dilemma, that a wider pelvis is less efficient during bipedal locomotion because it increases the work required by the hip abductors to counteract the rotation of the trunk during the single-leg-support phase of walking (Dunsworth et al., 2012; Wall-Scheffler, 2012; Warrener et al., 2015). Studies of male and female locomotion have, in fact, revealed a very similar level of efficiency in the two sexes, despite wider female bi-acetabular breadth (Dunsworth et al., 2012; Warrener et al., 2015). A small increase in the width of the female pelvic canal would substantially increase the area available for the passage of the foetus, while it would be unlikely to cause any significant rise in energy expenditure during walking and running. If this is the case, constraints on the size of the pelvic canal may not stem from a conflict with locomotion requirements.

A study by Huseynov and colleagues (2016) recently suggested that evolutionary constraints on the increase of the distance between the ischial spines, which would alleviate foeto-pelvic disproportion, might be due to the need to provide support for abdominal organs instead of increased locomotory efficiency. In fact, important ligaments and fascias that form the pelvic floor are anchored to the ischial spines (Abitbol, 1998).The authors also highlighted how pelvic shape changes during an individual's life, whereby canal dimensions reach a peak during the female most fertile years (around 20-40 years of age), followed by a slight decrease in canal size at the level of the ischial spines in the postmenopausal period. These female-specific shape changes over the life cycle might indicate long-term adaptation to ensure obstetric sufficiency during fertile years.

Obstetric sufficiency can, indeed, be expected to be under strong selective pressure. Complications during childbirth can lead to the death of the newborn and of the mother, or cause damage that could make future births difficult. As such, the impact on the mother's fitness is potentially extremely high. Considering that childbirth mortality and morbidity are not insignificant in modern populations, especially when hospital care is not available (Kolawole et al., 1978; Oxorn, 1986; Cottingham and Royston, 1991; Abou Zahr and Wardlaw, 2004; Dolea and AbouZhar, 2004; Hogan et al., 2010), it is surprising that our species has not evolved a larger birth canal.

Grabowski (2013) hypothesized that a possible reason for the tight fit observable in modern women could be that there has simply not been enough time for the pelvis to adapt to the very rapid increase in encephalization that occurred in Middle Pleistocene hominins (Ruff et al., 1997; Rightmire, 2004), possibly due to a higher level of genetic constraints on the pelvis in respect to neonatal cranial size (Grabowski, 2013).

Another possible explanation is that the tight fit observed today is a relatively recent consequence of a change in diet and environmental conditions. Differential phenotypic plasticity (i.e. the capacity for phenotypic changes in response to environmental changes) in the pelvis and in neonatal size might mean that the likelihood of foeto-pelvic disproportion varies depending on contingent environmental condition. Wells et al. (2012) suggest that the fit between neonate and canal became tighter after the development of agriculture. The

decreased protein intake and increased glycemic load associated with the change in subsistence would have resulted in lower adult stature of the mother but higher neonatal weight, therefore exasperating what was originally a close, but not as tight, fit. The recent shift towards a highly-calorific diet could have exasperated further the situation. If plasticity is at the root of the problem, the obstetrical dilemma might not be a dilemma after all. The size of the canal evolved to be sufficient in previous environmental conditions, and selection is now catching up with the change in circumstances.

Kurki (2007) noted that the KhoeSan population of South Africa, who tend to have a relatively small body size, appear to have a larger-than-expected birth canal when compared to bigger-bodied populations. The dimensions involved have obstetric significance, indicating that the selective pressure for a spacious birth canal could be particularly strong in small-bodied populations, possibly because the head of the newborn is not isometrically scaled according to the mother's body size, and is relatively larger than in bigger-bodied populations (Wells et al., 2012). The size of the canal might be protected in human populations, despite its large variability in shape (Kurki, 2013b). Indeed, the foetal head is quite plastic, due to the fact that the cranial bones are not fused and to the presence of the fontanelles, and it can partially adapt its shape while negotiating the mother's birth canal (e.g., Stewart and Philpott, 1980; Kriewall and McPherson, 1981).

Shorter-than-average mothers appear to have a higher probability of birth complications in various human populations (e.g., Tsu, 1992; Kwawukume et al., 1993; Witter et al., 1995; Cnattingius et al., 1998; Prasad and Al-Taher, 2002; Sheiner et al., 2005) due to more frequent mismatch between the size of the neonate and the size of the pelvic canal. The probability of a mismatch is reduced in part by the fact that neonatal head size tends to be inherited from the mother, so that small mothers with a small head tend to give birth to small-headed babies (Leary et al., 2006). In addition, females with a larger head, who are more likely to give birth to babies with a larger head, tend to have a rounder, obstetrically more capable birth canal (Fischer and Mitteroeker, 2015). A rounder birth canal is also more likely in shorter women, who are at higher risk of cephalo-pelvic disproportion (Fischer and Mitteroeker, 2015). This set of correlations indicates long-term selective pressure due to obstetric requirements.

Despite some evidence of obstetric-related selection, the ample variation in the shape of the pelvis and of the birth canal in modern women, both within and among populations, also brings into question the obstetrical dilemma as a strict compromise between locomotion efficiency and obstetric sufficiency. If strong evolutionary constraints due to a shared selective pressure (i.e. bipedal locomotion) were acting on the pelvis, we would expect to find low variability in the shape of the pelvic structure; however, not only does the birth canal shows a higher shape variation than other areas of the pelvis (Kurki, 2013b), but women are not less variable than men in this respect (Tague, 1989, 1995; Arsuaga and Carretero, 1994, LaVelle, 1995, Betti et al., 2013; Kurki, 2013b).

Human populations show ecogeographic variation in pelvic shape

Beyond early studies of racial variation in the pelvis, which highlighted differences between races in the shape of the pelvic canal (e.g., Turner, 1886; Caldwell and Moloy, 1933) and of the ilium (Derry, 1923; Straus, 1927), more recent studies have confirmed significant variation in pelvic shape between populations. Işcan (1983) and Patriquin et al. (2002) found that it was possible to set apart individuals of 'white' and 'black' ancestry based on a set of pelvic measurements with an accuracy of over 80%. Weaver and colleagues examined variation in the whole articulated pelvis in several human populations using 3D landmark coordinates, and were able to show that modern populations vary significantly in overall pelvic shape (Weaver, 2002; Weaver and Hublin, 2009). Similar results were obtained by Betti et al. (2014), who focused on the 3D shape of the ilium in a large number of populations. Wells et al. (2012) compared several studies on skeletal and in-vivo pelvic canal measurements and were able to show that high variation between populations is also present in the birth canal.

Variation in pelvic breadth among populations, in particular, has been noted and discussed by several authors (e.g., Ruff, 1991, 1993, 1994; Holliday and Hilton, 2010, Kurki, 2013a). Populations from higher latitudes tend to have relatively wider bi-iliac breadth than populations from lower latitudes, suggesting that part of the variation might be related to climate. There is abundant evidence that populations living in different climates tend to have different body proportions, with cold-adapted populations having relatively larger and stockier bodies, and populations in hot climates having smaller or more elongated bodies with relatively longer limbs (Schreider, 1950, 1964, 1975; Newman, 1953, 1961; Roberts, 1953, 1978; Baker, 1960; Coon, 1962; Crognier, 1981; Ruff, 1994, 2002; Holliday, 1997a,b, 1999, 2002; Katzmarzyk and Leonard, 1998; Weaver, 2002; Weaver and Steudel-Numbers, 2005; Weinstein, 2005; Tilkens et al., 2007; Weaver and Hublin, 2009, Betti et al., 2012, 2015). This pattern is widespread in endotherm animals, with closely related species displaying larger body sizes and shorter extremities in colder environments, and it is often referred to as Bergmann's (1847) Rule (for body size) and Allen's (1877) Rule (for body and limb proportions).

Homo sapiens evolved in Africa, where most regions are characterised by a warm or hot climate. For endothermic species such as humans, maintaining a stable body temperature in hot environments requires efficient heat dissipation; this is achieved in our species through sweat evaporation at the body surface, which is facilitated by a high body surface-to-volume ratio. The relatively elongated body shape of most sub-Saharan African populations in respect to other human populations, and the associated higher surface-to-volume ratio, has been interpreted as a thermoregulatory adaptation to a warm environment (Ruff, 1994, 2002; Holliday and Falsetti, 1995; Holliday, 1997a; Holliday and Hilton, 2010). After the expansion out of Africa and the colonisation of high latitude regions, it has been suggested that natural selection favoured more robust and stocky bodies with a lower surface-to-volume ratio, which helped maintain internal body temperature in cold climates. Differential climatic adaptation might therefore have contributed in generating modern population

differences in body proportions, body size, limb robusticity, and even pelvic shape (Trinkaus, 1981; Ruff, 1991, 1994; Holliday and Falsetti, 1995; Pearson, 2000; Stock, 2006; Weaver and Hublin, 2009).
Kurki (2013a) compared nine populations from various continents, and found a relationship between latitude and canal shape, whereby high-latitude populations tend to have a transversally wider midplane and outlet and an inlet which is less deep antero-posteriorly than mid- and low-latitude populations. Betti et al. (2014) and Weaver (2002) found a significant relationship between temperature and the 3D shape of the ilium and of the whole pelvis, suggesting that both pelvic and canal shape have been partially shaped by local climatic adaptations, possibly through the effect of natural selection favouring thermally efficient body sizes and proportions.
It is possible, and indeed it has been suggested before (e.g., Ruff, 1994, Weaver and Hublin, 2009, Kurki, 2013a), that thermoregulatory adaptations in the shape of the pelvis generated a different type of conflict with obstetric requirements: another form of 'dilemma'. The narrower body favoured in hot and humid environments could limit the transversal width of the birth canal, increasing at the same time the anterior-posterior diameter in order to preserve a minimum size for the passage of the foetus; on the contrary, the wider body common in cold regions could translate into a more transversally-elongated shape of the canal at higher latitudes. This interpretation could help make sense of the geographic variation in the pelvic canal recognised since early racial studies, taking into account, at the same time, shared obstetric requirements and constraints.
In addition to climate, several other factors are thought to contribute in generating pelvic shape variation within and between human populations. For example, nutritional deficiencies and disease, sometimes associated with low social status, as well as activity, age and number of pregnancies, have been shown to have an influence on skeletal and pelvic size and shape (Greulich et al., 1939; Nicholson, 1946; Thoms, 1946, 1947; Krukierek, 1951, 1954; Bernard, 1952; Angel, 1978; Kelley, 1978; Holland et al., 1982; Micozzi, 1982; Abitbol, 1987; Kelley and Angel, 1987; Stuart-Macadam, 1989; Sibley et al., 1992; Bogin et al., 2002; Bogin and Rios, 2003, Specker and Binkley, 2005; Schutz et al., 2009, Huseynov et al., 2016). However, these factors are expected to explain differences between individuals within a population more than differences between populations, except in case of substantial and systematic differences in diet, lifestyle or health between certain populations.

Evolvability of the pelvis and the effects of past population history

In a comparative study of the primate pelvic girdle, Grabowski (2013) examined the pattern and strength of covariation between pelvic measurements in different species. He found a significantly smaller covariance in the dimensions of the human pelvis compared with other closely related species. This result is surprising in the light of the fact that humans experience a tighter cephalo-pelvic fit during childbirth in respect to other apes (Abitbol, 1991; Rosenberg and Trevathan, 2002), a fact that should hypothetically translate into stronger evolutionary constraints on the size and shape of the female pelvic canal.

Grabowski and colleagues (Grabowski et al., 2011; Grabowski, 2013) interpret the lower human covariance as the outcome of the shift to bipedalism, whereby a release of constraints allowed for a substantial rearrangement of the shape of the hominin pelvis in australopithecine or earlier species. The decrease in covariance comes with an increase in the evolvability of the pelvic structure, which is freed from previous constraints and more susceptible to change (Grabowski, 2013). Lower covariance also means that it is relatively easier for structures to evolve independently of other structures, so that different sets of traits could evolve in response to different selective pressures.

Middle Pleistocene hominins showed a rapid increase in encephalization from around 500 ky years ago (Ruff et al., 1997; Rightmire, 2004), leading to a tight cephalo-pelvic fit in humans and Neanderthals. Obstetric requirements were fulfilled in different ways in the two later Pleistocene species, probably taking advantage of the relatively high pelvic evolvability. Neanderthal females achieved a large pelvic canal thanks to a more elongated pubic ramus (Rosenberg et al., 1988). Neanderthal and modern human birth canals differ also in the geometry of the three pelvic planes. Although different reconstructions of the only fairly complete Neanderthal female pelvis, Tabun C1, have been put forward, it seems likely that Neanderthals preserved the ancestral transverse orientation of the main diameter of the outlet, therefore presenting a different pattern of childbirth from modern humans (Weaver and Hublin, 2009; but see Ponce de León et al., 2008). The changing pattern of covariance between pelvic traits over hominin evolution, and the likelihood of indirect effects of selection on covariant traits, means that it is crucial to use a multivariate approach to understanding the evolution of pelvic morphology (Rolian, 2014; Grabowski and Roseman, 2015; Grabowski, 2016).

The lower level of covariance and a relatively higher evolvability in the human pelvis could help explain the large shape variation observed within and among modern populations. The lack of strong evolutionary constraints on pelvic shape helps make sense of why, against expectations due to obstetric selective pressures, the pelvic canal shows high variability, and that the level of variation is the same in males and females.

Low constraints on the pelvis can also explain the clear ecogeographic pattern in pelvic shape observed in human populations, despite the fact that their recent dispersal into colder environments offered only a short time for evolution to act. The greater freedom of pelvic traits to change independently on each other offers a wider range of possible shapes that can evolve quickly without disrupting the whole pelvic structure. This freedom returned a high diversity within-population, which is the ideal basis for directional selection to improve adaptation to different environments.

A higher magnitude of pelvic evolvability also offers a wider scope for genetic drift to increase phenotypic differences between populations. Our species is relatively young, probably not much older than 200-250 ky old, and went through a rapid range expansion of a global scale in the last 100-60 ky (e.g., McDougall et al., 2005; Mellars, 2006; Armitage et al., 2011; Eriksson et al., 2012; Fu et al., 2013). The rapid geographic expansion was accompanied by a reduction in genetic diversity with increasing distance from the continent

of origin, Africa (Prugnolle et al., 2005, Ramachandran et al., 2005). This loss of diversity is evident in both genetic and phenotypic variation, such as cranial and dental shape variation (Manica et al., 2007, Hanihara, 2008; von Cramon-Taubadel and Lycett, 2008; Betti et al., 2009), and is the natural consequence of genetic drift when a series of founder events occur. Each subpopulation which colonised a new area carried only a portion of the genetic diversity present in the source population, thereby generating the described pattern of gradual decrease of genetic variation.

A similar decline in phenotypic variation with distance from Africa has been identified in the os coxae (Betti et al., 2013; Fig. 3). The signature of the species' expansion appears to be even stronger on the pelvis than on the cranium, with distance from sub-Saharan Africa explaining up to about 47% of within-population variance (Betti et al., 2013), a fact that indicates that modern variation in the os coxae has been significantly affected by genetic drift.

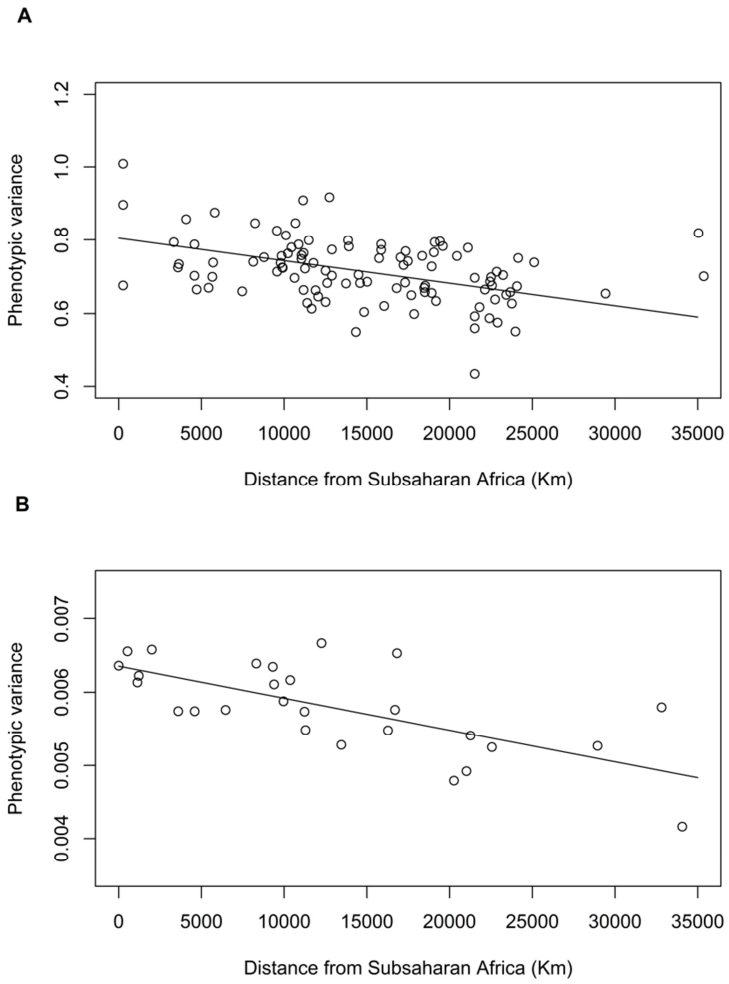

Fig. 3. Plots of within-population phenotypic variance against geographic distance from sub-Saharan Africa for the cranium (A) and the os coxae (B). Data from Betti et al., 2009, 2013.

As human range expansion followed divergent routes into the various continents, it might be expected that genetic drift led to a random shift in average pelvic shape along the main

directions of expansion. In fact, shape differences in the os coxae among populations appear to increase with geographic distance along those different routes (Betti et al., 2014) (Fig. 4). The colonisation of new areas and subsequent exchange of migrants between populations are expected to generate a geographic pattern of variation, with nearby populations showing closer genetic and phenotypic resemblance than populations more distant in space. This pattern is due to the fact that closer populations are more likely to have emerged from a recent common ancestral population during the expansion of our species; in addition, geographic proximity favours gene flow between populations and increases similarity (Imaizumi et al., 1973; Cavalli-Sforza et al., 1994; Eller, 1999; Relethford, 2004b). Both the cranium and the pelvis show a similar pattern, with geographic distance explaining about 30-35% of between-population shape variance (Betti et al., 2010, 2014; see also Roseman, 2004; Harvati and Weaver, 2006a; Hubbe et al., 2009; von Cramon-Taubadel, 2009a).
In comparison, climatic adaptation plays a significant, but smaller role. Differences in climate explain up to about 18% of coxal shape variation among populations, which is reduced even further once the variation explainable by neutral processes is taken into account (Betti et al., 2014). Climate, on the other hand, seems to have a stronger effect on coxal size, with minimum temperature explaining up to 43% of size variation (Betti et al., 2014).

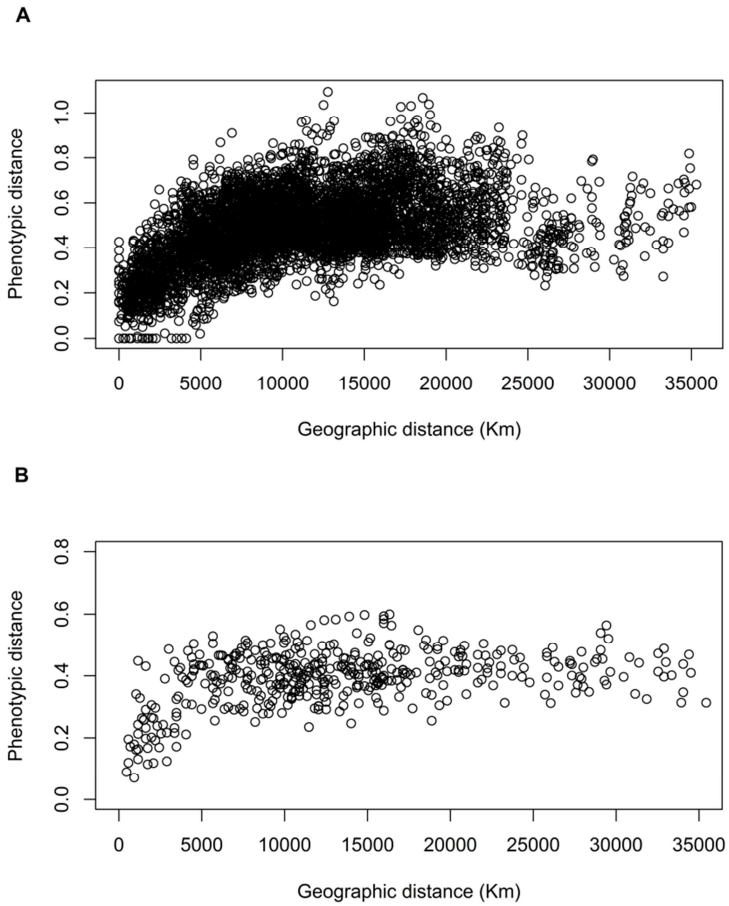

Fig. 4. Plots of between-population phenotypic distance against geographic distance for the cranium (A) and the os coxae (B). Data from Betti et al., 2010, 2014.

Pelvic sexual dimorphism also appears to have been affected by past demographic events (Betti, 2014). Shape differences between the sexes are not stable across human populations, but vary geographically. Part of this geographic diversity in sexual dimorphism (about 15%; Betti, 2014) can be explained, again, by population history.
Although the amounts of variance explained by neutral factors need to be considered as purely indicative, stochastic processes due to genetic drift and differential migration clearly played an important role in shaping pelvic differences between populations. Climatic adaptation acted over this underlying neutral pattern, affecting both pelvic size and shape. The comparison between the effects of climatic adaptation and past population history, however, suggest that the latter had a larger influence on pelvic – or at least, coxal – shape variation. The importance of neutral processes is also reflected in the global pattern of apportionment of pelvic shape variance. As for neutral genetic markers and cranial shape, pelvic shape diversity between populations and between continents is much smaller than the average diversity within single populations (Betti et al., 2013). The opposite is true for skin colour, for example, whereby strong directional selection increased the variance among regions well beyond the variance within populations (Relethford 2002).
Acknowledging that a substantial portion of phenotypic variance in modern populations is the outcome of neutral processes is important for at least two reasons. First, it provides an explanation for morphological differences which are not clearly related to local adaptations. Second, it affects the way we test for natural selection. Adaptation due to natural selection is often inferred from a significant correlation between the factor of interest and morphology. However, environmental factors are usually partially correlated with geographic distance, due to the fact that nearby areas tend to share similar environmental conditions. As morphological distance also tends to be correlated with geographic distance, because of neutral demographic processes, a significant correlation between morphological traits and environmental factors could be due, at least in part, to collinearity with geographic distance. In other words, the underlying neutral pattern of variation could confound the analyses and generate spurious correlations with environmental factors. Roseman and Auerbach (2015) showed very eloquently how this problem can impact on tests of climate-related selection on the human postcranium.

Conclusions

The view of the pelvic girdle as a strict compromise between two opposite selective pressures, a narrow bi-acetabular distance for efficient bipedal locomotion, and a wide pelvic canal for easy parturition, has been challenged (Dunsworth et al., 2012; Wall-Scheffler, 2012; Warrener et al., 2015). The wider female pelvic breadth is not associated with less efficient locomotion, calling into question the elegant hypothesis of an “obstetrical dilemma”. This finding leaves open the question of why a wider female pelvic canal has not evolved in our species, given the significant risk of childbirth mortality and morbidity due to cephalo-pelvic disproportion and the subsequent decrease in fitness. One possible explanation is that the modern sedentary lifestyle and the availability of highly calorific food

enjoyed by many populations has exacerbated the risk of childbirth complications by increasing average neonatal size (Wells et al., 2012). If that were the case, the hypothesized selective advantage of a larger birth canal would be a recent phenomenon.

These studies not only cast doubt on the existence of an obstetrical dilemma, but also on the existence of strong evolutionary constraints on the pelvic structure, which would be the logical extension of the obstetrical dilemma hypothesis. Indeed, the pelvis and the pelvic canal do not show low morphological variation in respect to other parts of the skeleton, as would be expected under strong evolutionary constraints (Kurki, 2007, 2013a,b; Betti et al., 2014). On the contrary, it appears that the human pelvis in under lower constraints than other closely related primates, showing lower covariance between its parts and a higher level of evolvability (Grabowski, 2013; Grabowski et al., 2011).

The evidence of low evolutionary constraints on the pelvis help make sense of the wide diversity in pelvic and pelvic canal shape observed in modern human populations. A relatively high evolvability means that a larger range of possible shapes can evolve in a shorter time, since it can provide more variation upon which both natural selection and drift can act. The rapid expansion of our species out of Africa into higher latitudes and colder environments exposed human populations to new selective pressures, which could have contributed to the geographic variation in pelvic shape observable today. In fact, the wider pelvis of high-latitude populations and the narrower bodies of tropical populations have been interpreted as a thermoregulatory adaptation (Ruff, 1991, 1993, 1994; Holliday, 1997b; Holliday and Hilton, 2010, Kurki, 2013a). Differences in body size in human populations could also have been accompanied by increased selective pressure for obstetric capacity, leading to a relatively larger and deeper birth canal in small-bodied populations (Kurki, 2007).

A substantial portion of pelvic variation among modern populations has been shaped by neutral evolutionary processes, such as genetic drift and distance-mediated gene flow (Betti et al., 2014). In the study of human evolution and diversity, there has been a tendency to interpret skeletal variation as the direct effect of natural selection, employing an adaptationist approach, while the effects of neutral processes have been largely ignored. Several recent studies, on the other hand, have highlighted the potential impact of random genetic drift in hominin evolution (e.g., Weaver et al., 2007, 2008; Ackermann and Cheverud, 2004) as well as modern human variation (e.g., Relethford, 1994, 2002, 2004a; Roseman, 2004; Roseman and Weaver, 2004; Harvati and Weaver, 2006; Smith, 2009, 2011; Betti et al., 2009, 2010, 2014; von Cramon-Taubadel, 2009a, 2009b, 2011; von Cramon-Taubadel and Weaver, 2009; Strauss and Hubbe, 2010). Despite that fact that adaptation narratives have an undeniable appeal, the less interesting random accumulation of differences due to genetic drift and differential migration is an ever-occurring process and can potentially explain a large portion of phenotypic variation between human populations.

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